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SPATIAL PATTERNS AND BEHAVIOR OF YEARLING MALE BLUE GROUSE AND THEIR RELATION TO RECRUITMENT INTO THE BREEDING POPULATION

by

© IAN G. JAMIESON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Abstract

Movements and behavior of yearling male Blue Grouse (*Dendragapus obscurus*) equipped with radio transmitters were monitored during spring and summer, 1980 and 1981, on Hardwicke Island, British Columbia. Most yearlings associated with territories occupied by adult males. Others settled near vacant sites that had been used as territories in previous years and a few did not localize but moved widely over the breeding range. Variation among birds may be the result of differences in territory quality. Presumed costs and benefits associated with these three types of spatial patterns are outlined.

Spatial patterns and behavior of yearling males changed as the breeding season progressed. Both size of home ranges and number of visits to territories of adult males decreased and birds appeared to be aggregating late in the summer. Yearlings showed some seasonal fidelity to territories with which they associated in early spring, but there was considerable variation among individuals. The number of sexual and aggressive interactions involving yearling males also decreased as the breeding season advanced. Changes in spatial patterns and behavior appear to be related to changes in levels of aggression.

During the day, yearling males were primarily inactive, remaining in or near vegetative cover, moving very little and feeding occasionally. At dusk, however, birds were very active in the open. In spring, when levels of aggression are highest, some yearlings may have been initiating interactions with females and territorial adult males but avoiding birds of their own age and sex and those with non-breeding status. Only one of 24 yearlings showed territorial behavior. Results from this study support the "sexual bimaturism" hypothesis to explain why yearling males of promiscuous species usually do not breed even though yearling females do.

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INTRODUCTION

Recent research on Blue Grouse (*Dendragapus obscurus*) on Vancouver Island, British Columbia, has been primarily aimed at determining how breeding densities are regulated. Males are rarely territorial in their first year; rather, these birds act as a population reserve by filling in vacancies, in subsequent years, that are left by territorial adults that die. Information on mechanisms controlling recruitment of yearling males into the breeding population should, therefore, contribute to our understanding of how breeding densities of adult males are determined.

Sopuck (1979) suggested that yearlings may interact among themselves and that spacing behavior may limit the number of potential recruits. If dispersion is the consequence of spacing, and if some yearlings are preventing others from settling, then variation in spacing patterns of individuals may result and perhaps give some birds an advantage in securing a territory. My objectives were to examine the behavior and spacing patterns of yearling males and to see how these might relate to recruitment. Results are presented in three papers:

1. Spatial patterns of yearling male Blue Grouse and their relation to recruitment into the breeding population.
2. Seasonal changes in spacing patterns and behavior of yearling male Blue Grouse on the breeding range.
3. Time budget and behavior of yearling male Blue Grouse and their relation to delayed breeding and recruitment.

In the first paper, I examine variation among individuals in spacing patterns, particularly in relation to territories of adult males. In the second paper, I document seasonal changes in spacing patterns and interactions with conspecifics, and discuss the causal mechanisms and possible adaptive significance of these changes. In the third paper, I examine the behavior of yearling males, in particular, interactions with conspecifics, and attempt to interpret these data in relation to subsequent recruitment. Here, I discuss the concept of delayed breeding in first-year males.

BACKGROUND

Most Blue Grouse breed in open areas at low elevations. These open areas have been created by clear-cut logging and burning of the refuse.

All available evidence indicates that Blue Grouse are promiscuous. They come onto breeding ranges in late March and early April. Adult males establish territories and sing (hoot) regularly from early April well into June. Most yearling males do not hold territories or sing.

Nesting normally commences by early May, and most chicks are hatched between early and late June. Practically all adult and most yearling females participate in breeding, but yearlings are generally less productive than adults.

Blue Grouse on Hardwicke Island appear to differ from those on Vancouver Island in that some do not migrate from breeding areas to winter, but remain on the same range year round. Those that migrate, do so by mid- to late August.

I. Paper 1. SPATIAL PATTERNS OF YEARLING MALE BLUE GROUSE AND THEIR RELATION TO RECRUITMENT INTO THE BREEDING POPULATION

A. Abstract

Movements of yearling male Blue Grouse (*Dendragapus obscurus*) were monitored by radio telemetry during the springs of 1980 and 1981, on Hardwicke Island, British Columbia. Locations of yearlings were clumped around territories of adult males. Most birds associated with a few occupied territories, others settled near vacant sites that had been used as territories in previous years and a few moved widely over the breeding range. Some territories attracted more yearlings than others and it appears that there may be competition among yearlings for these sites. Presumed costs and benefits associated with three types of spatial patterns shown by yearling males are discussed.

B. Introduction

First-year males of many polygynous and promiscuous species are rarely territorial (Wittenberger 1978). Rather, these birds act as a population reserve by filling in vacancies, in subsequent years, that are left by territorial adults that die. Information on mechanisms controlling recruitment of yearling males into the breeding population should contribute to our understanding of how breeding densities of adult males are regulated, yet few workers have studied potential recruits in detail.

Blue Grouse are considered promiscuous (Wiley 1974). Yearling males usually do not hold territories and presumably do not breed (Bendell and Elliott 1967), even though they produce viable sperm (Hannon et al. 1979). Young adults establish territories in the same general area they occupied as yearlings (Sopuck 1979; Jamieson unpubl. data). However, removal studies indicate that more yearling males are present on the breeding range than are necessary to replace adult males that die (Bendell et al. 1972; Zwickel 1972, 1980). Whether acquisition of a vacant site is a matter of chance, or whether some other factor(s) such as behavior, genetics, or size, allows some males to gain an advantage in establishing a territory as an adult is unknown.

Zwickel (1980) suggested that spacing behavior among yearling male Blue Grouse may limit the number of two-year olds that are available as recruits. If some yearlings prevent others from settling, and if dispersion is the consequence of spacing, then I predict variation in spacing patterns among individuals. If yearlings are surveying potential breeding sites, they may be located near territories of adult males and this could give some birds an advantage in subsequently securing a vacant site.

One problem associated with studying non-territorial birds is that they are often secretive. Radio telemetry helps to alleviate this problem since one can obtain repeated locations of individuals at will. In 1980-81, I monitored the movement of yearling male Blue Grouse equipped with radio transmitters to try to determine how dispersion of these birds might relate to recruitment as adults. Yearlings did show variation in their spacing patterns and I speculate on how these differences might affect subsequent survival and fecundity.

C. Study Area and Methods

The study area was on Hardwicke Island, off the east-central coast of Vancouver Island, British Columbia, approximately 3 km north-east of the town of Sayward. A 460 ha area served as the main study site (HI-1). In 1980 only, additional information was collected from birds on a subsidiary area (HI-2).

Both study areas were clear-cut between 1968 and 1973. Vegetative structure ranged from "very open" (Bendell and Elliott 1967), consisting primarily of burned or unburned slash, mixed grasses, fireweed (*Epilobium angustifolium*), salal (*Gaultheria shallon*), and red huckleberry (*Vaccinium parvifolium*); to "open", consisting mainly of western hemlock (*Tsuga heterophylla*) and Douglas fir (*Pseudotsuga menziesii*) 3 to 7 m in height. Douglas fir occurred mainly in plantations.

Experimental birds were initially found with the help of trained pointing dogs and captured with noosing poles (Zwickel and Bendell 1967). They were equipped with solar-powered or battery-powered transmitters using a harness similar to that of Herzog (1977). Birds were caught either in late summer as juveniles, 2-3 months old, or in the following spring as yearlings, 10-11 months old. The "backpack" units weighed approximately 22 g, 2-4% of the body weight of the bird, depending on the age at capture.

Movements of 10 and 14 yearling males were monitored in 1980 and 1981, respectively, from the third week in April to the third week in June. Other studies indicate this period to be most important in relation to recruitment (Sopuck 1979; Jamieson 1982a). Not all radios worked consistently, especially solar-powered transmitters. However, most birds were located at least once every two days whenever possible. Sightings of banded, non-radio-tagged yearling and adult males were also available as a result of concurrent studies in the area.

"Exact" locations were determined by sighting individuals and pacing to known reference points. "Estimated" locations were determined by triangulation from within 100 m of a bird. Both types of locations were used in analyses except for data involving distances from territories of adult males; here only exact locations were used.

Home ranges were depicted on maps by the minimum area method (Harvey and Barbour 1965) and their size was measured with a polar planimeter. The entire area used

by territorial males cannot be accurately determined by general census procedure because too few sightings are obtained for each male. However, males spend most of their time in a few specific sites within their territories; these sites have been referred to as activity centers (McNicholl 1978; Lewis unpubl. MS). I plotted the geographic center of the locations of each male by the method of Hayne (1949) and termed these the activity centers of territorial males.

I use "territory" to mean the area that is occupied, and presumably defended, by a male for displaying to and copulating with females (Bendell and Elliott 1967). A "territorial site" is the place where a territory is, or had been, located; it may not be occupied every year (Lewis and Zwickel 1981).

D. Results

On average, birds were located every 1.9 days (range= 1.2–4.8) and a median number of 34 (range= 8–55) locations were obtained for each male.

Distance from Territories of Adult Males

If yearling males are surveying potential breeding sites, then one might expect their locations to be clumped around territories of adult males. I measured the distance from each location of a yearling male to the activity center of the nearest territory. I compared these to the mean distance of random points to the activity centers of nearest territories (Table 1). In both years, yearling males on HI–1 were, on average, significantly closer to activity centers of adult males than expected from a random distribution (t–test; t=6.0(1980) 4.1(1981); $p < 0.001$). Birds on HI–2 were also significantly closer to activity centers than expected (t–test; t=2.4; $p < 0.01$) but individuals there were further away from activity centers than those on HI–1 (ANOVA; F=13.5; $p < 0.01$). Reasons for this difference are not known, and the three birds on HI–2 were omitted from the following analysis.

Yearling males varied significantly in the distances they were found from activity centers of territories of adult males (ANOVA; F=1.8; $p < 0.05$). Mean distances from activity centers for individuals on HI–1 were similar in 1980 and 1981 (ANOVA; F=1.4; $p > 0.10$); therefore the variation among individuals was not due to year. Although there was a gradient in mean distances, there appeared to be behavioral differences between the six birds that stayed furthest from activity centers and those yearlings that were closer (Table 2). Here we must examine individual case histories. Three yearlings (672, 130, 694) localized in areas with no occupied territories in the immediate vicinity but near territorial sites that had been occupied the year before. If the locations of these individuals are measured to the activity centers of these territorial sites, their average distances from activity centers decrease and fall within the range of the other yearlings.

One yearling (801) was highly localized and singing, and therefore should be considered territorial (Bendell and Elliott 1967). This then explains his relatively large distance from other territorial males. There was one sighting of an adult male in this area the previous year but it is not known whether he was territorial.

Another yearling (625) localized in an area where there were no territories in the immediate vicinity and where none were known the year before. Unlike for any other yearling, the nearest occupied territory was in mature timber where the resident adult usually sang high in a tree on the edge of the timber adjacent to where 625 had localized. Adult males actively exclude yearlings that are on or near their territories (Jamieson 1982b). If this male could detect intruders more easily than males that occupied territories on the ground, then the minimum distance that 625 could approach without being displaced might be greater than for other yearlings.

Yearling 703 maintained the greatest average distance from territories. He localized for only a brief period, then moved widely about the study area and had the second largest home range (32.8 ha) among all yearlings (median size of home range=10.8; range= 0.6–40.7).

A seventh yearling which had the largest home range (40.7 ha), was located on the study area only five times, and therefore was not included in the above analyses. That bird also moved widely. On one day he interacted with and was displaced successively by five different territorial males and one yearling (Jamieson 1982b). He was killed by a predator mid–way through the breeding period.

Association with Territories of Adult Males

In order to examine if yearlings were settling near particular territories, I had to define the distance that a location of a bird had to be from a territory for it to be considered "near". Arbitrarily, a location was said to be in the vicinity of a territory if its distance from the activity center of the territory was less than the average distance that random points were from activity centers (Table 1). For simplicity, any location of a bird meeting this criterion was termed a "visit" to a territory. An "association" with a territory describes a bird that had a larger proportion of visits to that territory than would be expected from an equal distribution among all territories visited by that yearling. The frequency of visits for specifying an association was usually significant at the 5% level (Binomial Test, Siegel 1956). However, significance was easier to demonstrate for birds that had a large proportion of visits to one territory than for those with most of their visits distributed among a few territories. This was due to the relatively small number of

locations obtained for each yearling. Thus, I did not require that the number of visits specifying an association be statistically significant.

If yearlings were attracted to territories of adult males, how many territories, on average, did they associate with during the breeding period? Sixty percent of the 160 territories visited by yearlings received only one to two visits while 20% received more than four (Figure 1). For 22 yearlings, the median number of territories each visited was nine (range=3–17), and the median number of territories with which they associated was two (range=0–6). There was a positive correlation between size of home range and number of territories visited (Spearman's Rank Correlation Test; Rho=0.5; $p < 0.05$) but no correlation between size of home range and number of associations (Rho=0.2; $p > 0.10$). Although most yearlings associated with at least one territory, some associated mainly with unoccupied sites, as noted above.

The fates of only three of seven yearlings that were believed to be alive at the end of the 1980 breeding season are known, as six of the transmitters did not operate in the spring of 1981. For the four that were not resighted, 10 of the 11 territories with which they had associated were reoccupied (in 1981) by the previous territory holder. If any of these birds had taken territories elsewhere, then there was a high probability that they would have been found by census crews, but a low probability of finding them if they were not territorial or had died during the winter.

Of the three birds resighted, one associated with three territories in 1980. Two of the residents returned but the third did not, and this bird occupied his site in 1981. Another established a territory on a previously unoccupied site. He had associated with two occupied territories in 1980, of which neither resident returned in 1981. However, those two territories were on either side, and in close proximity to the territory he subsequently occupied, and most of his locations as a yearling were closer to this site. Therefore, sightings near the other two territories may have been coincidental. This male was killed on his territory by a predator in early spring. The third bird associated with two occupied territories in 1980. Both were reoccupied by the same males in 1981 and he was sighted several times as a non-territorial two-year old.

Association with Territories in Relation to Other Yearlings

Although individual yearlings are associating primarily with a few territories; some territories may attract more than one. To examine this question, I searched a 50 ha area in early spring, 1981, and all yearling males caught were equipped with radios. Seven yearlings, all of which were used in some of the previous analyses, were captured on this plot. The area was censused intensively for most of the breeding period, and during this time, only two other yearlings were sighted (each only once); both were on the edge of the area. Therefore, I assumed all resident yearlings on the plot were radio-tagged.

I wanted to examine the dispersion of birds on a day-to-day basis. To compare locations of a number of individuals found at different times of the day, I had to determine the extent to which birds were moving. Fifty times during the study, a bird was located twice on the same day. The median distance moved per hour was 2 m (range=1-24). Since movement appeared minimal during the day (see also Jamieson 1982b), locations of individuals on any one day were assumed to be fixed points for this analysis.

Home ranges overlapped to a high degree (Figure 2) and yearlings were usually (15 of 17 days) distributed randomly over the area (Clark and Evans Nearest Neighbour Analysis; $R=0.71-1.5$; $p > 0.10$ for 15 days). The median distance from any bird to his nearest neighbour was 210 m (range=18-637).

The seven yearlings varied in their number of associations with territories (Figure 3). One moved widely over the area and another was territorial; both had no associations. Another associated with one territory but had even more sightings near an unoccupied site; this yearling was killed by a predator on this site on 18 May. The four other yearlings had from two to four associations, and each had one to three associations in common with another yearling. Furthermore, on 14 occasions two birds from this group were found less than 100 m apart on the same day. In 10 of these cases, the two were visiting the same territory and in eight of these, both had a common association with that particular territory.

There were 18 territories on this area. Most of these (83%) had none or one yearling associating with them; only a few had two or three (Figure 4). It appears that some territories attract more yearlings than others.

E. Discussion

Some workers have suggested that site-specific experience of non-territorial males may be important in subsequent attempts to establish a territory. Yasukawa (1979) found that in first-year Red-winged Blackbirds (*Agelaius phoeniceus*), site-specific experience might produce delayed benefits by enhancing the probability of eventual recruitment. Non-breeding male Rufous-collared Sparrows (*Zonotrichia capensis*) restrict their movements to a few occupied territories and establish linear hierarchies within these. When the breeding male dies, the dominant male quickly fills the vacancy; experience within the territory seems necessary for successful acquisition (Smith 1978). Guillon (1967) noted that yearling male Ruffed Grouse (*Bonasa umbellus*) are frequently seen near drumming sites of adult males, and that they will occupy these sites if the resident male disappears.

Data from two previous telemetry studies with Blue Grouse showed that yearling males were found on territories less frequently than expected during the day (Lance 1970; Sopuck 1979). Based on these results, Lance and Sopuck suggested that yearlings might be avoiding territories of adult males. My study shows that when the dispersion of birds over the entire breeding area is considered, locations of yearlings are clumped around, though not necessarily on, territories of adult males during daytime hours.

Not only were yearlings found closer to territories of adults than expected but most associated with only a few territories. My behavioral observations indicate that yearlings may interact with residents on these sites, mainly at dawn and dusk, perhaps assessing site quality by testing the ability of the male to defend his territory (Jamieson 1982b). However, not all radio-tagged birds associated with occupied territories, as some settled near vacant sites that had been used as territories in previous years. One of these appeared to be territorial, although this is probably rare (Bendell and Elliott 1967).

Two birds moved widely over the study area and one was eventually killed by a predator. Greater movement may result from not being able to settle in areas already occupied by other yearlings. Sopuck (1979) suggested that yearlings that move widely may be subject to high predation pressure. Three of the 30 yearling males that he followed did not localize and were killed by predators.

One factor that may be important for successful territorial establishment by two-year olds is that sites must become vacant within the home range a bird used as a yearling. Most of the replacements in a removal experiment on Blue Grouse were by non-territorial adult males, many of which presumably would not have taken territories unless sites were made available (Lewis and Zwickel 1980). Nine of 10 replacements that were banded as yearlings or non-territorial adults had been previously sighted within 1 km of the removal site that they subsequently occupied (Jamieson and Zwickel, unpubl. data).

Of the birds resighted as adults in my study, one replaced a territorial male that did not return, one established a territory on a previously unoccupied site, and another was non-territorial, having associated with two territories as a yearling, to which both occupants returned in 1981. Although some birds that were not resighted may have died, others could have been non-territorial since they had associated with territories that were reoccupied by previous residents.

In the portion of the study area where I marked all resident yearlings, some birds did not associate with any occupied sites while others associated with the same two or three territories, perhaps resulting in competition for these sites. Yearlings will displace others, and site-related dominance may be important in determining which birds replace adult males that fail to return to their territories (Jamieson 1982b).

Why do some territories attract more yearlings than others? Lewis and Zwickel (1981) found that adult males preferred certain territorial sites over others. Territories were either occupied each year (persistent sites) , or used intermittently (transient sites). There were twice as many transient as persistent sites, and approximately one-half of the transient sites were vacant in any given year. Males on persistent sites survived longer and had more females near their territories during peak breeding. Furthermore, both non-territorial adult and yearling males preferred persistent sites when both types were made available in a removal experiment (Lewis and Zwickel 1980). This latter point suggests that birds can assess territorial quality.

My study area has only been censused for three years, so background data are insufficient to distinguish between persistent and transient sites. However, if territorial sites vary in quality, as suggested by Lewis and Zwickel (1981), then yearlings may

compete for certain territories, especially if there are fewer high quality than low quality sites. Considering this assumption, I have outlined some costs and benefits which may be associated with three different patterns of dispersion shown by yearling male Blue Grouse (Table 3).

There may be a number of reasons why Blue Grouse usually do not show territorial behavior as yearling males even though there are always some territorial sites available (Jamieson 1982b). These reasons are based on Wiley's (1974, 1981) hypothesis that yearlings delay breeding in order to increase chances of early survival and later fecundity. One consequence of my predictions (Table 3) is that most non-territorial two-year olds must have exhibited a type 'A' pattern, and the high quality sites with which they had associated were reoccupied the following year. Therefore, Wiley's idea may also apply to adults, if some two-year olds delay breeding in order to wait for a high quality site to become available. However, since life expectancies decline with age, it may not be advantageous for birds older than two years to delay taking a territory (Lewis and Zwickel 1981). Older males should then be expected to settle on low quality sites if high quality sites are not available.

Finally, not all yearlings may be able to compete equally for high quality sites, and it may be more advantageous for these birds to associate with low quality sites. However, it should not be assumed that yearlings showing 'Pattern A' dispersion will have a greater fitness than birds showing 'Pattern B' (Table 3). Although the benifits of associating with a high quality site are high *once* one of these territories is secured, the cost associated with this type of dispersion as a yearling may also be high. Among individuals, costs related to competition may depend on dominance ranking of birds while costs related to turnover rates of territorial adults on high quality sites may depend more on chance.

Since birds using both high and low quality territories appear to be well established in the population (Lewis and Zwickel 1981), it is probable that yearlings selecting either strategy have, on average, equal fitness. However, further data are needed on differential mating success of males occupying high and low quality territories before this question can be resolved.

F. Acknowledgements

Sincere thanks are due to F.C. Zwickel for introducing me to this study, providing field support, and for his stimulating discussions. J.O. Murie, G.H. La Roi, and L. Fedigan contributed helpful comments on the thesis. J. Hines, R.A. Lewis, H. Speed, L. Maslen, and many summer assistants aided in the field.

Funding was by the Natural Sciences and Engineering Research Council, the Canadian National Sportman's Fund, the B.C. Fish and Wildlife Branch, and the University of Alberta. The study was conducted on lands of Crown Zellerbach of Canada Limited and Bendickson Contractors and their cooperation is greatly appreciated.

Table 1. Comparison of mean distances (m ±S.E.) that random points and locations of yearling males were from activity centers of the nearest territories of adult males. Only birds with 10 or more locations were included. The number of random locations was equivalent to the number of territories that were on the study areas each year.

Year	Study Area	Random Locations	Yearling Locations
1980	HI-1	N=150	N=61 (4 birds)
		$\bar{X}$=89±4	$\bar{X}$=58±5
	HI-2	N=37	N=48 (3 birds)
		$\bar{X}$=103±7	$\bar{X}$=83±5
1981	HI-1	N=124	N=247 (12 birds)
		$\bar{X}$=83±4	$\bar{X}$=65±2

Table 2. Mean distances that yearling males were located from activity centers of the nearest territories of adult males. Sample sizes for individuals are in parentheses.

Yearling No. (N=16)	Mean Distances (m ±S.E.) From Activity Centers
106	46±7 (16)
633	49±7 (17)
1	54±8 (21)
678	55±6 (22)
220	58±7 (18)
695	59±5 (31)
47	59±8 (14)
135	60±7 (12)
696	64±5 (39)
31	65±18 (10)
672	71±8 (18)
625	75±10 (12)
130	76±8 (14)
694	79±11 (12)
801	79±7 (10)
703	83±9 (17)

Table 3. Presumed costs and benefits associated with three patterns of dispersion shown by yearling male Blue Grouse.

Pattern A	Association with high quality territories
Costs-	High degree of competition for these sites
	- Low rate of turnover of territorial males (few vacancies)
Benefits-	Survival and fecundity rates are high on these sites
Pattern B	Association with low quality territories
Costs-	Survival and fecundity rates are low on these sites
Benefits-	Little or no competition for these sites
	- High rate of turnover of territorial males
Pattern C	Move widely about the breeding range and do not associate with any territories
Costs-	High mortality rate?
	- Low probability of breeding
Benefits-	None known

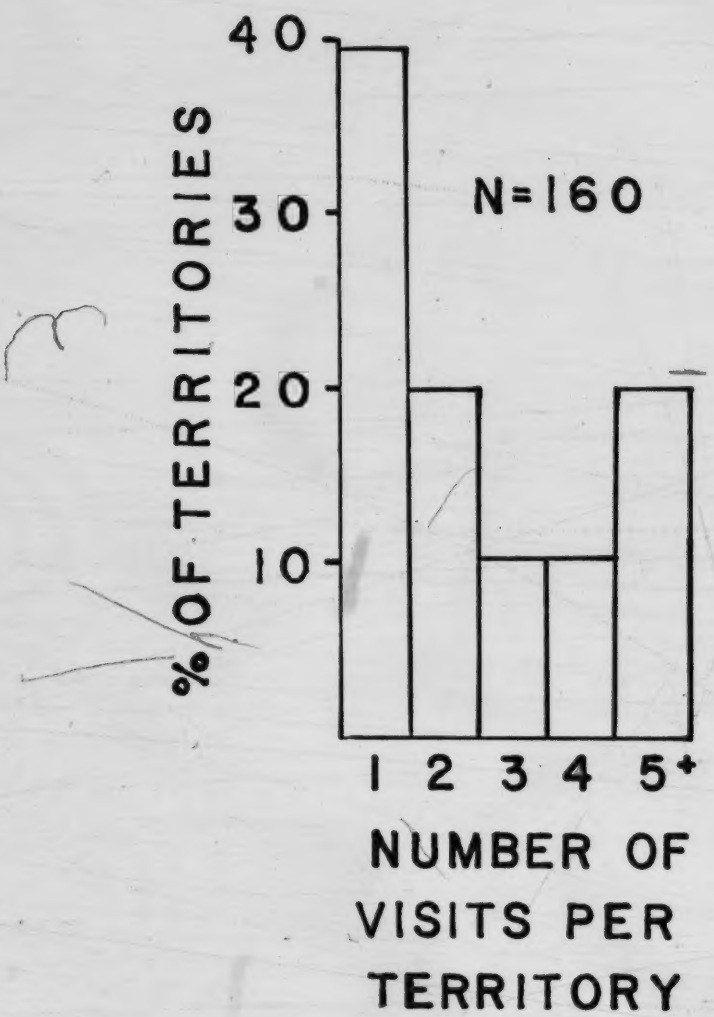

Figure 1. Frequency distribution of territories visited by yearling males grouped according to the number of visits per territory.

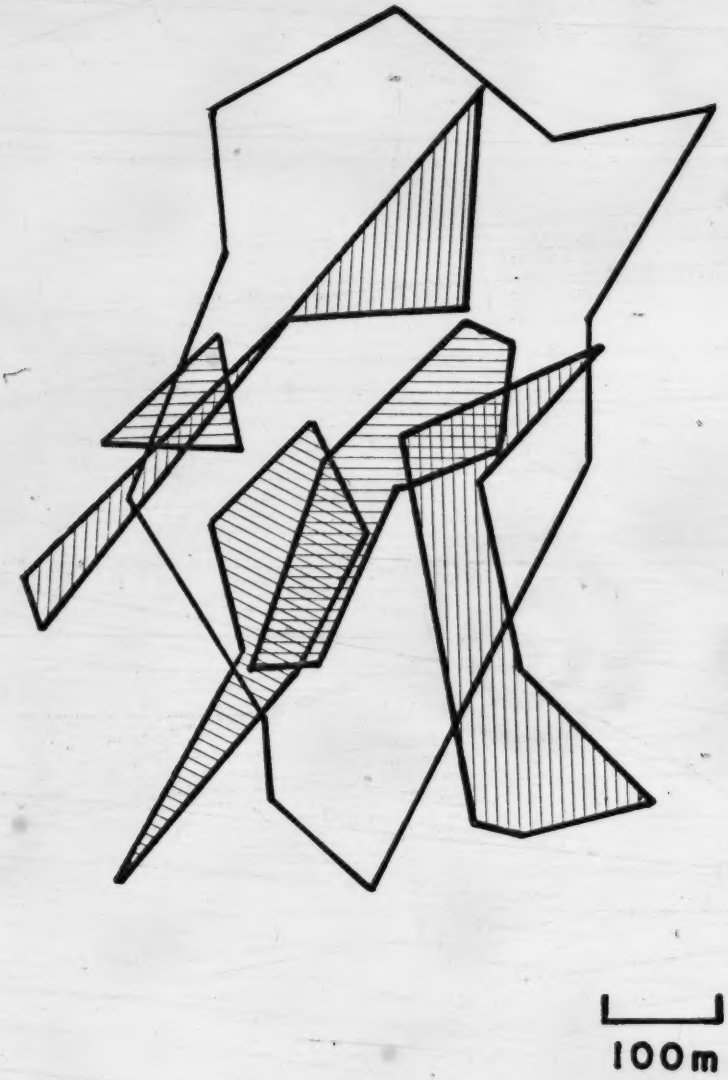

Figure 2. Home ranges of six yearling males on one section of the study plot.

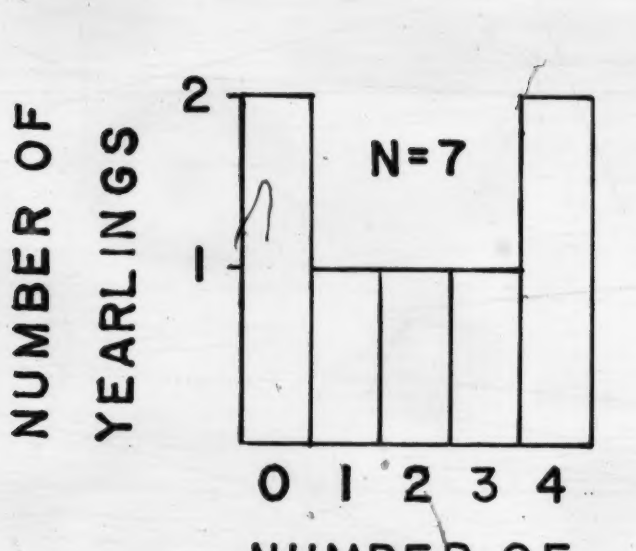

Figure 3. Frequency distribution of yearling males grouped according to the number of associations each had with territories of adult males.

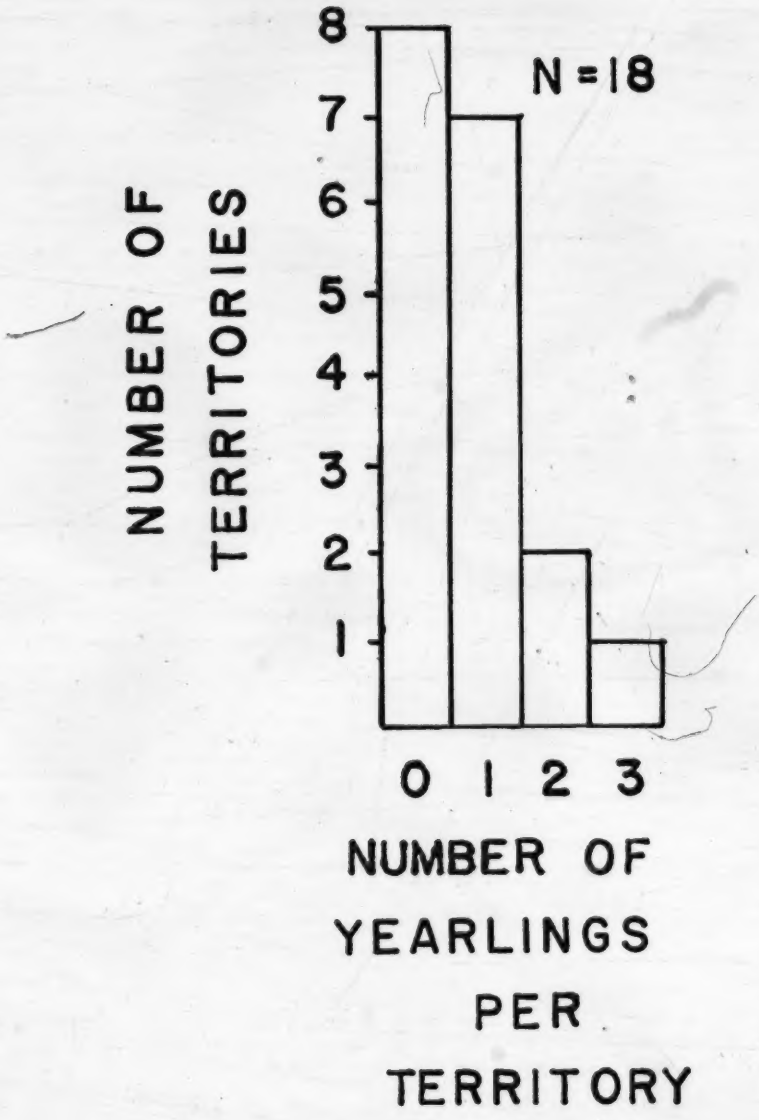

Figure 4. Frequency distribution of territories grouped according to the number of yearling males associating with each territory.

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II. Paper 2. SEASONAL CHANGES IN SPATIAL PATTERNS AND BEHAVIOR OF YEARLING MALE BLUE GROUSE ON THE BREEDING RANGE

A. Abstract

Changes in spatial patterns and behavior of yearling male Blue Grouse (*Dendragapus obscurus*) equipped with radio transmitters were monitored during the spring and summer, 1980 and 1981, on Hardwicke Island, British Columbia. The study period was divided into four seasonal periods, early spring, late spring, early summer, and late summer, based on changes in the gonad cycle of yearling males. Both size of home ranges of yearlings and the number of visits to territories of adult males decreased as the season progressed. Most remained on their initial home ranges until late summer, at which time birds began to aggregate. Yearlings showed seasonal fidelity to territories with which they associated in early spring but as with most other aspects of spacing, there was variation among individuals. The percentage of interactions involving yearling males and females decreased as the season advanced. Interactions involving yearling males and territorial males also decreased, but to a lesser extent. No sexual or aggressive interactions were observed in early or late summer. Changes in spatial patterns and behavior appear to be related to seasonal changes in levels of aggression of yearling males.

B. Introduction

Changes in behavior in response to changes in the reproductive cycle have been reported for a number of species (Lehrman 1961; Emlen and Miller 1964; Fisler 1969). Many animals exhibit a different spatial pattern during reproductive and non-reproductive phases of the year. Fisler (1969) suggested that it might be adaptive for animals to use different patterns under changing physiological conditions. Although some studies have documented seasonal changes in territorial behavior in birds (Weeden 1965; Stefanski 1967; Peek 1971), little has been published on seasonal changes in spacing behavior of non-territorial individuals.

First-year male Blue Grouse are rarely territorial (Bendell and Elliott 1967) but appear to localize around territories of adult males in spring, perhaps to increase their chances of subsequent establishment on a territory (Jamieson 1982a). Substantial changes in the testicular cycle of yearling males occur from the time they arrive on the breeding range in early spring until they migrate to winter range in late summer (Hannon et al. 1979). Thus, first-year males might show different patterns of use of space on the breeding range at different times of the season.

In 1980-81, I monitored the movement of yearling male Blue Grouse equipped with radio transmitters to determine whether seasonal changes in spatial patterns occurred on the breeding range. Changes in three aspects of spatial pattern were examined. These were: size of home range, frequency of visits to territories of adult males, and fidelity to specific areas and territories. Changes in the frequency of interactions with conspecifics were also examined. Both causal mechanisms and adaptive significance of seasonal changes in spacing are discussed.

C. Study Area and Methods

The study area was situated on Hardwicke Island, off the east-central coast of Vancouver Island, British Columbia, approximately 3 km north-east of the town of Sayward. A 460 ha area that was clear-cut between 1969 and 1973 served as the main study site. Details of vegetative structure are described elsewhere (Jamieson 1982a).

Experimental birds initially were found using trained pointing dogs and were captured with noosing poles (Zwickel and Bendell 1967). They were equipped with either solar-powered or battery-powered transmitters using a harness similar to that of Herzog (1977). Birds were captured either in late summer as juveniles, 2-3 months old, or in the following spring as yearlings, 10-11 months old. The transmitter weighed from 2-4% of the body weight of the bird, depending on age at time of capture.

Movements of 24 yearling males were monitored using portable telemetry equipment during 1980 (N=10) and 1981(N=14). For purposes of analysis, the study was divided into four seasonal periods which correspond to changes in the gonadal cycle of yearling males (Hannon et al. 1979). The cycle, which is based on volume of testes and intertubular tissue, shows; a peak in *early spring* from about two weeks after yearlings arrive on the breeding range, around the third week in April, to the third week in May; a slow decline in *late spring* from the fourth week in May to the third week in June; a rapid decline in *early summer* from the fourth week in June to the third week in July; and a low in *late summer* from the fourth week in July to the third week in August. By late August, most yearling males in this population had commenced migration to winter range (Jamieson unpubl. data). Only birds located at least seven times during a given period were included in any analysis. Intensive observations of individual birds were conducted during early and late spring only. Details of methods used for behavioral observations are given in Jamieson (1982b).

Not all transmitters worked consistently, especially solar-powered radios. However, most birds were located at least once every two days. Sightings of banded, but not radio-tagged, yearling and adult males were also available as subsidiary information from other, concurrent studies.

Locations were determined by sighting a bird and pacing to known reference points, or estimating the location by triangulation from within 100 m ; all locations were

plotted on grid maps. Home ranges of yearlings were depicted by the minimum area method (Harvey and Barbour 1965), and their size determined with a polar planimeter.

A "visit" to a territory refers to a location of a yearling male at a distance from the activity center of a territory that was less than the distance from activity centers determined from a random distribution of locations. An "association" with a territory refers to a bird that had a larger proportion of visits to a particular territory than would be expected from an equal distribution among all territories visited by that yearling (see Jamieson, 1982a, for further explanation of these terms).

D. Results

The number of yearlings that were located seven or more times varied for each seasonal period. Twenty-three birds were monitored in early spring, 18 in late spring, 16 in early summer, and 13 in late summer. The median number of locations per yearling for each period was 20 (8-24), 16 (11-27), 13 (7-19), 14 (9-16), respectively. Eleven individuals were monitored during all four seasonal periods.

Changes in Spatial Patterns

Median size of home range declined for individual yearlings as the season progressed (Friedman's Trend Test; $Z=-2.05$; $p< 0.05$) (Figure 1). Variation among individuals in size of home ranges increased from early spring to late spring and early summer, then declined.

To what degree did yearlings show fidelity to specific areas in different seasons? Birds were considered to have remained on the same area if more than 50% of their locations during a given period were located within the home range occupied during a specified previous period. Sixty-seven percent (12/18) and 62% (10/16) of the individuals in late spring and early summer, respectively, remained on the same areas they had occupied in early spring. By late summer, only 23% (3/13) remained where they had been in early spring.

Birds also appeared to be more aggregated late in the season. In early summer, the centers of home ranges of five yearlings located in a 76 ha area were, on average, 1013 m ± 131 S.E. (range=738-1345) apart. In late summer, these same yearlings were all found in a 3.4 ha area, and the centers of their home ranges were, on average, only 89 m ±6 (range=65-107) apart.

Not all yearlings moved to new areas at the same time. Median date of movement off initial home ranges for 16 birds was 14 June but ranged from 16 May to 29 July; one stayed in the same general area throughout spring and summer.

Locations of yearling males appeared to be clumped around territories of adult males during early and late spring (Jamieson 1982a). However, individuals showed a significant downward trend in the percentage of visits to territories from early spring to early summer (Friedman's Trend Test; $Z=-2.14$; $p< 0.05$) (Figure 2) but an increase in late

summer. Again, variation among individuals increased after early spring.

The territorial sites with which yearling males associate in spring appear to be areas where they attempt to establish a territory as two-year olds (Jamieson 1982a). Thus, I examined the extent to which yearlings continued to associate with the same sites throughout the season. Eight of the 11 individuals that were monitored for all four seasonal periods associated with new territories in late spring (Table 1). By early summer, three had returned to the territories they associated with in early spring, but by late summer, nine were associating with new territories. Thus, yearlings vary in seasonal fidelity to territories with which they had been associated.

Changes in Frequency of Interspecific Interactions

Since the gonadal condition of yearling males changes with seasonal period, one might expect to see changes in their behavior toward conspecifics. In particular, changes in aggressiveness toward other males and sexual responsiveness toward females might occur. Yearlings courted or attempted to court females on 16 occasions in early and late spring. The percentage of observations involving interactions (any incident where the behavior of a bird changed in response to the presence of a nearby conspecific) with females was greatest in early May and then decreased (Figure 3); numbers of interactions were too few for statistical treatment. On two occasions, 4 and 6 June, a female flew and landed within 30 m of a yearling but the male did not respond.

Yearling males were involved in 34 agonistic encounters with other males in early and late spring; 30 of these were with territorial males. The frequency of interactions with adult males also declined over time, but not to the same degree as with females (Figure 3), perhaps because adult males were the aggressors, and because they defend their territories against intruders late in the season (Lewis unpubl. MS). However, on eight occasions a yearling may have initiated an interaction with an adult male by making direct and conspicuous movements onto a territory (Jamieson 1982b); these all occurred between 18 April and 31 May.

Although no intensive observations were conducted in early or late summer, a yearling was found with a female or another male four and nine times, respectively, during these periods; six of the nine males were other yearlings, the remainder were of

unknown age. However, no sexual or aggressive behaviors were seen in these situations. In one case, two radio-tagged yearlings were feeding together on 23 July, and neither exhibited overt hostility toward the other, even though they had engaged in an aggressive interaction earlier in the season (15 May).

E. Discussion

Patterns of dispersion in yearling male Spruce Grouse (*Canachites canadensis franklinii*) changed seasonally, and maximum spacing occurred during the period of intense breeding (Herzog and Boag 1978). Spacing patterns of yearling male Blue Grouse also appear to change during the season. Before discussing these changes and their relevance, I would like to examine what causes these changes.

Trends in dispersion, home range, and activity in non-territorial Deer Mice (*Peromyscus maniculatus*) appear closely related and these are greatly influenced by high levels of aggression early in the breeding period (Metzgar 1979). Aggression appears to be correlated with changes in hormone levels (Trobec and Oring 1972; Watson 1970). In Blue Grouse, volume of testes and amount of intertubular tissue, which reflect hormone levels, show a decline from early spring to the period of migration (Hannon et al. 1979). Therefore, changes in pattern of dispersion of yearling males may in part result from changes in levels of aggression.

In early spring, during the peak breeding period, home ranges of yearlings were relatively large compared to those in the latter part of the season. The decrease in size of home ranges is probably the result of a decrease in activity of yearlings which is related to a decline in their responsiveness toward conspecifics. Behavioral observations described elsewhere (Jamieson 1982b) show that during early and late spring, yearlings intruded on territories of adult males, usually resulting in their displacement by the resident male. First-year males flew toward and courted females. Also, yearlings were almost always alone, and when seen together, they always interacted agonistically. However, the frequency of sexual and aggressive interactions decreased as the season advanced, and birds became more social. During early, but particularly late summer, individuals often were found in close association with each other, and no overt hostility was evident.

What is the adaptive significance of having different spacing patterns at different times of the year? Early in the breeding period, birds may be surveying territorial sites to which they may subsequently recruit as adults and therefore, the number of visits to territories is relatively high. Furthermore, spacing behavior among yearlings may occur as a result of competition for certain sites (Jamieson 1982a). If hormone levels decrease,

causing a decline in aggressiveness, individuals birds no longer may be motivated to space themselves in relation to territories or conspecifics. Yearlings then seem to form small groups, perhaps for protection against predators (Wiley 1974). Such clumping requires some birds to move off their home ranges to locate other yearlings. Most adults have left their territories by late summer (Lewis unpubl. MS.), so yearlings would be able to move onto those areas without being displaced. That may explain why visits to territories increased in late summer (Figure 2).

Although yearlings may space themselves in relation to territories of adult males in early and late spring, it is not clear why some birds are still associating with the same territories in early summer. Yasukawa (1979) suggested that first-year male Red-winged Blackbirds (*Agelaius phoeniceus*) begin to occupy and defend territories after the mating period in order to gain experience in the area where they will attempt to establish a territory the following spring. Late in the breeding season, adult male blackbirds are primarily concerned with interspecific territorial defense in order to protect their mates and their young, and ignore yearling males on their territories (Nero 1956, Peek 1971). Yearling male Blue Grouse did not show similar behavior, probably because adult males defend their territories against other males relatively late in the breeding season. However, if site-specific experience is important for subsequent establishment of a territory, then a yearling may gain some advantage by associating with the same territory late into the breeding period. Yet in one case in this study, a two-year old established a territory where he had localized as a yearling in early spring, even though he moved approximately 1.5 km to a new area after this period. In this case, prolonged site attachment did not seem necessary for subsequent establishment. Sopuck (1979) found that in a population of Blue Grouse on Vancouver Island adult males were still on their territories after most yearling males had migrated to winter range.

Spatial patterns changed as the breeding period progressed but not all yearlings appeared to change at the same rate or to the same extent. This was especially apparent in the timing of yearlings leaving their initial home ranges and probably caused the increased variation that was noted among individuals within and between seasonal periods. Adult males show similar variation, as 10 territorial birds equipped with radios left their territories and moved to new areas between 17 June and 11 August (Lewis

unpubl. MS).

As for variation of adult males with respect to remaining on their territories, there is no clear explanation of why some yearlings associate with particular territories late into the breeding season while others do not (Table 1). Whether birds that stay in one area are associating with prime sites (Jamieson 1982) and/or are increasing their chances of breeding the following year is not known.

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Financial support was provided by the Natural Sciences and Engineering Research Council, the Canadian National Sportsman's Fund, the B.C. Fish and Wildlife Branch, and the University of Alberta. Work was conducted on lands of Crown Zellerbach of Canada Limited and Bendickson Contractors.

Table 1. Seasonal fidelity of yearling males to territories of adult males with which they had associated in previous periods. Rows indicate seasonal periods in which yearlings had an association that was the same as one in the specified period (column heading). 'New' indicates that a yearling associated with territories with which he had not been associated previously.

No. of Yearlings (N=11)	Seasonal Periods		
	L.Spr.	E.Sum.	L.Sum.
2	E.Spr.	E.Spr.	New
1	E.Spr.	New	New
1	New	E.Spr.	E.Spr.
2	New	E.Spr.	New
1	New	L.Spr.	E.Spr.
1	New	L.Spr.	New
3	New	New	New

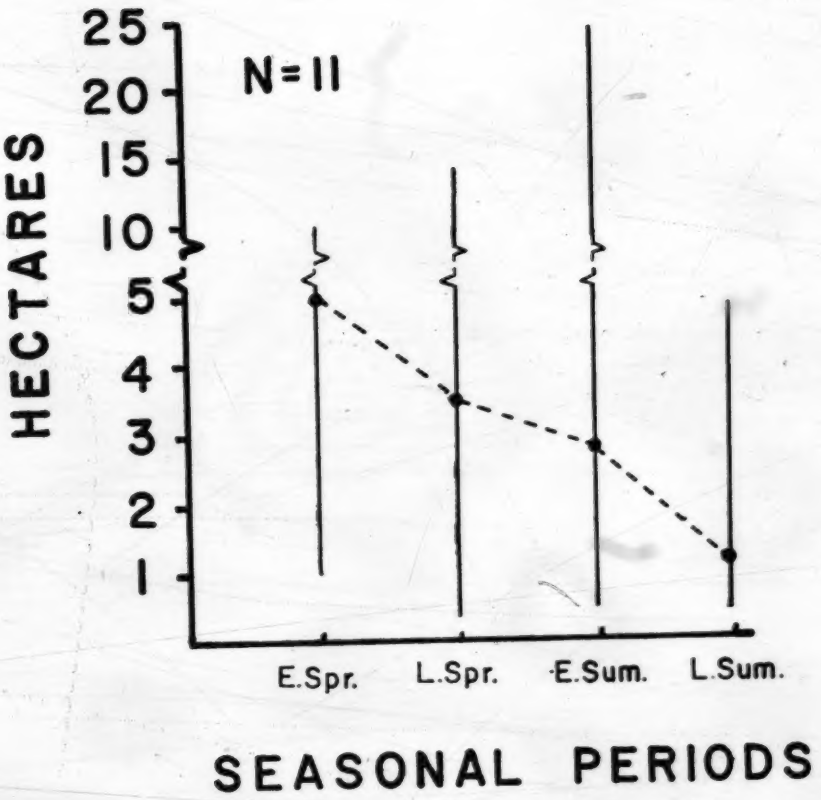

Figure 1. Median size of home ranges of 11 yearling males for each seasonal period. Ranges are indicated by vertical lines.

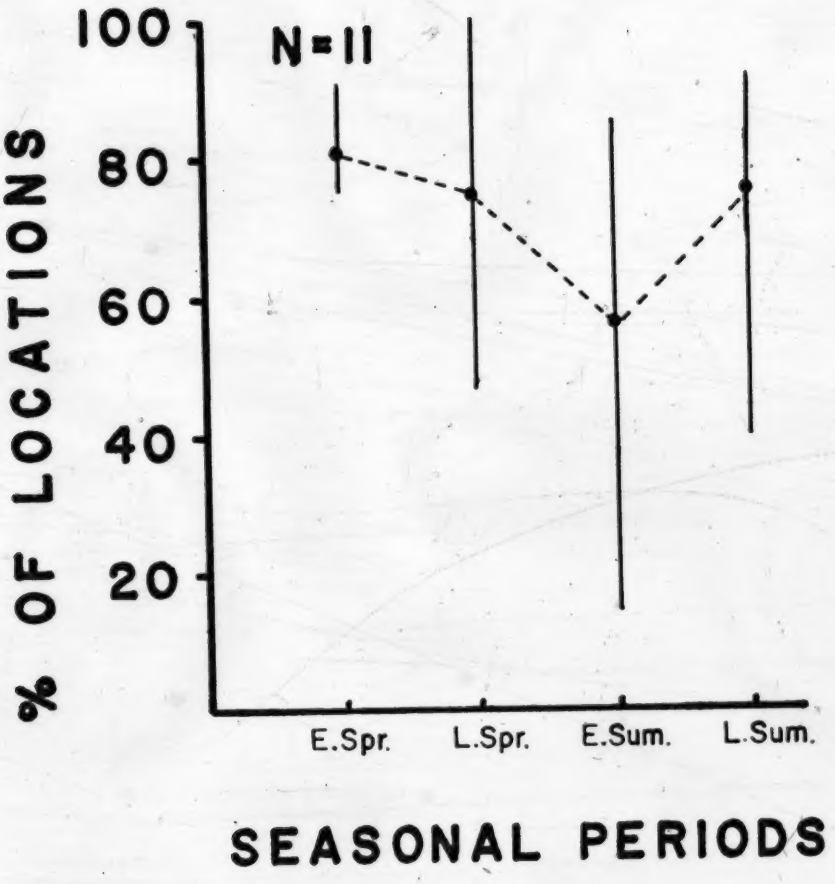

Figure 2. Number of visits by 11 yearling males to territories of adult males expressed as median percentage of the total number of locations for each seasonal period. Ranges are indicated by vertical lines.

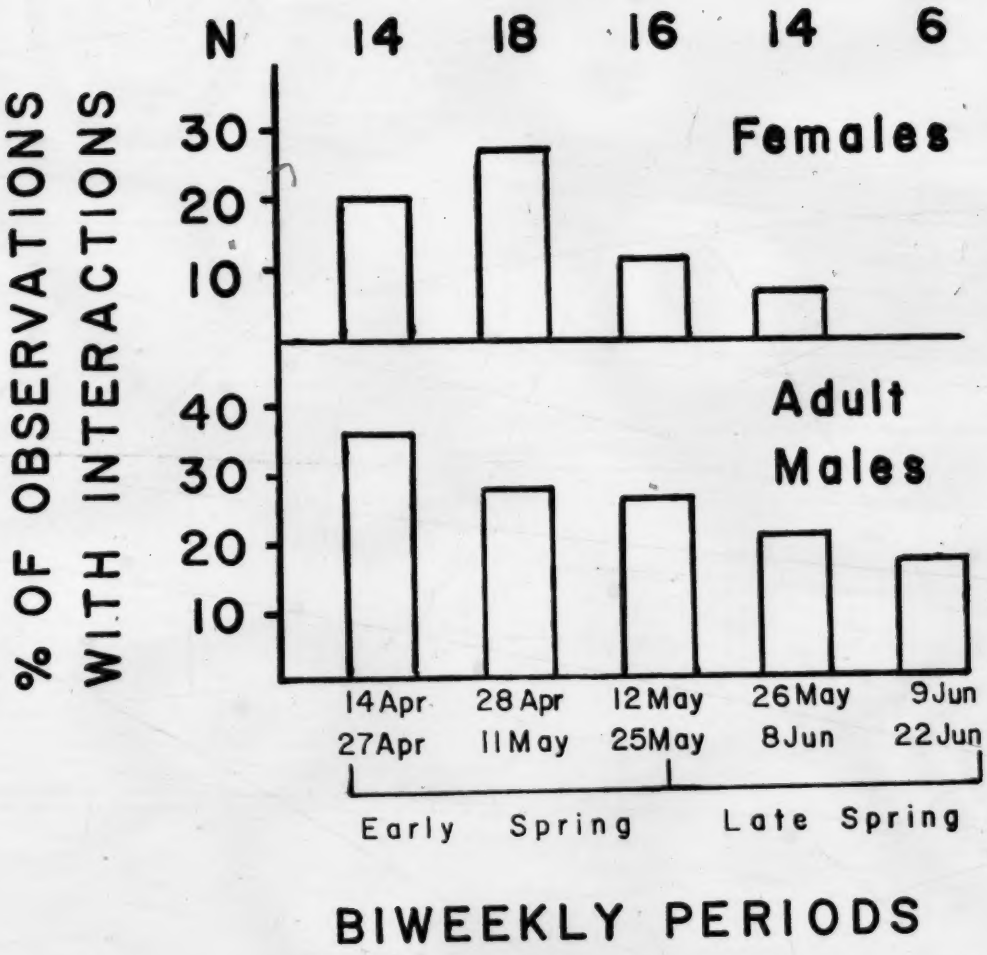

Figure 3. Percentage of obsérvational sessions in which at least one interaction occurred between a yearling male and a female or an adult male during early and late spring. The number of sessions for each biweekly period is indicated by N. Only observational sessions conducted during the evening, when birds are most active, (see Jamieson 1982b) are included.

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III. Paper 3. TIME BUDGET AND BEHAVIOR OF YEARLING MALE BLUE GROUSE AND THEIR RELATION TO DELAYED BREEDING AND RECRUITMENT

A. Abstract

A study of the time budget and behavior of yearling male Blue Grouse (*Dendragapus obscurus*) was conducted on Hardwicke Island, British Columbia during the springs of 1980 and 1981. Birds were sedentary three-quarters of the time, usually in or near thickets during the day, and were overtly active only for short periods, primarily at dawn and dusk. Yearlings were observed to interact with adult males (25 times), other yearling males (4 times), females (11 times), and both females and adult males (5 times). It appeared that some yearling males initiated interactions with females and territorial males but avoided birds of their own age and sex and those of non-breeding status. Birds displayed to, and courted, females but did not show the full range of courtship behaviors given by adult males. They made no attempts to copulate. Only one of 24 yearlings showed territorial behavior. Results from this study support the "sexual bimaturism" hypothesis to explain why yearling males of promiscuous species delay breeding while yearling females do not.

B. Introduction

Detailed demographic and behavioral work on Blue Grouse has been conducted on Vancouver Island, B. C., since 1950. Much of this research has focused on breeding females and adult males, and little detailed study has been done on the behavior of non-breeding, yearling males.

Although first-year males are usually non-territorial, they will occupy territories and presumably breed after the experimental removal of territorial adults (Bendell et al. 1972; Zwickel 1972, 1980). Therefore, yearlings may not be able to compete effectively with older, more experienced males for territories. Furthermore, adults displaced intruders, presumed to be yearling males, from their territories during play-back experiments (McNicholl 1978), although expulsion of yearlings from territories has been recorded infrequently in natural circumstances (Bendell and Elliott 1967; McNicholl 1978). Although adult males may limit the number of potential recruits that will enter the breeding population, Sopuck (1979) suggested that yearlings may interact among themselves and that this might be a mechanism which limits the number that eventually gain territories. To the best of my knowledge, however, interactions among first-year males have not been reported.

During the springs of 1980 and 1981, I observed yearling male Blue Grouse equipped with radio transmitters to gain more information on their behavior. The objectives of the study were: 1) to describe the behavior of yearling males during the breeding season, 2) to see if yearling males interacted with territorial adult males and other yearlings, and 3) to interpret any such interactions in relation to recruitment into the breeding population. I also discuss delayed breeding in yearling male Blue Grouse as it relates to current theory.

C. Study Area and Methods

The study area was situated on Hardwicke Island, off the east-central coast of Vancouver Island, British Columbia. For a general description of the study site, and methods used to capture and radio-tag birds, see Jamieson (1982a).

Observations were conducted from 14 April to 22 June in both years. Aggression levels are thought to be highest at this time, based on the gonadal cycle of Blue Grouse (Hannon et al. 1979; see also Jamieson 1982b). Twenty-four yearling males were equipped with radios and observed intensively, and other yearlings were observed when opportunities allowed. Most other male and female Blue Grouse in the area had been individually color-marked as a result of other studies.

The ease with which a yearling could be observed varied with openness of the habitat. Since some birds were found in open habitat more frequently than others (Jamieson, unpubl. data), the number of times each yearling was observed varied. Observations were carried out from approximately 2 h after sunrise to darkness. Those conducted during the day were usually terminated after 1 h and another bird was located and observed. There was usually only enough time to locate and observe one bird during the evening.

The median distance from which birds were observed (with the aid of binoculars) was 20 m (range= 10-80) , using vegetation as natural blinds. If a bird appeared disturbed, an observational session did not begin until he appeared to assume normal behavior such as feeding or preening.

A time budget of activities and notes on behavior were recorded. Activity was divided into two major categories; stationary and moving. A bird was considered to be moving if his position changed more than 1 m in less than 60 s.

D. Results

Sixty-three and 58 observational sessions were conducted during 1980 and 1981, respectively, totalling 106 h of observational time. Twenty-four different males were observed, with a median of four sessions conducted on each (range= 1-14).

Time Budget and Diurnal Activity Patterns

Birds were classified as stationary for 74% of the observation time, during which they were either inactive (56%) or feeding (18%) (Figure 1). Moving, which involved the other 26% of the time budget, included three behaviors: feeding (15%), walking (5%), and interacting (6%).

At first sighting, birds were in the open, away from vegetative cover, only 30 of 171 times (18%). Birds that were located twice in the same day (N=50), moved a median distance of 2 m per h (range= 1-24) (Jamieson 1982a). Yearlings usually remained in or near thickets during the day, moved very little, and fed only occasionally.

The amount of time spent moving tended to decrease from early morning to mid-day, and increased from then until dark (Figure 1). At dusk, yearling males were more active, moving about in the open; birds would sometimes run in short bursts of 5-15 m (21 times), or fly short distances of 10-30 m (16 times) for no apparent reason. Twenty-three of 29 interactions (79%) noted during observational sessions occurred in the last two hours before sunset. Activity peaked in a 15-20 min interval around sunset, but on four occasions birds were still moving about at least 1 h after this.

Females and adult males also increased their activity at dusk. Furthermore, adult males are said to show a peak in activity at dawn (Bendell 1955). Although I did not conduct observations before sunrise, high activity of yearling males may occur at this time as well.

Intraspecific Interactions

Yearling males interacted with adult males, other yearling males, females, and females and adult males together.

I observed yearling males interacting with territorial males 25 times. Males that detected yearlings on or near their territories immediately assumed a display posture

(Stirling and Bendell 1970), then ran or flew towards the yearling. When 1–3 m from him, the adult assumed a threat posture (McNicholl 1978) in which the feathers were laid flat against the body, the tail was lowered, the eye combs were orange or red, and conspicuous white–shoulder patches were visible. The adult quickly moved back and forth in front of and around the yearling; he gave a "growl", an aggressive or threat call (Stirling and Bendell 1970), on 11 occasions. On two occasions a yearling was approached by an adult in full display with wings dragging on the ground; this is considered a courtship behavior (Stirling and Bendell 1970). When approximately 1–3 m from the bird, the adult assumed a threat posture and ran at and displaced the yearling. Both incidents occurred after sunset and the adult may have mistaken the yearling for a female under the poor light conditions.

Yearling males almost invariably assumed a neutral posture (McNicholl 1978) during encounters with adult males. On 10 occasions, they remained in this position for 10–30 s before flying from the area. One notable exception occurred on 27 May, 1980. A yearling that had been courting a female on the edge of a territory remained in full display when the resident adult male approached in threat posture. The adult immediately flew at, and pursued him for several meters before the yearling flew off. The yearling was found near the same territory the following day. During the breeding period, 71% of the locations (17/24) of this bird were within 90 m of the center of this territory.

I observed 12 cases in which an adult male rushed at a yearling and displaced him. However, I saw only one physical attack, which occurred on 24 May, 1981. An adult approached a yearling that was on his territory, moved around him for 80 s, then rushed at him and pecked his back, removing several feathers. The yearling ran approximately 100 m and took cover in dense vegetation.

In some cases it was difficult to determine what provoked interactions between yearlings and territorial males. On 10 occasions, yearlings were feeding and/or moving near a territory when the resident male flew towards and confronted them. Prior to each of these instances, I was not aware that an adult was in the immediate vicinity. However, on at least eight occasions between 18 April and 31 May, yearlings made direct movements of 20–250 m toward specific territories on which resident males were singing. Once near the territories, their movements and short flights made them

conspicuous, and adult males displaced them in every instance. These yearlings had been located frequently near these particular territories during the breeding period (Jamieson 1982a). One such incident is described below.

On 27 April, 1980, I found a yearling in a dense thicket approximately 50 m from an adult male who was singing; the adult was on a stump and was clearly audible and visible. At about sunset, 50 min later, the yearling moved into the open, flew 20 m, and landed in full view of the singing male. The territorial male immediately flew towards him and landed 7 m away in full display. The adult approached and when about 1 m from the intruder assumed a threat posture; the yearling remained in a neutral posture and after 15 s flew off.

On only four occasions did I observe two yearlings interacting with each other. Although encounters between yearlings appear to be rare, the consequences of such interactions could be important, perhaps in terms of site-dominance. Three such agonistic interactions are described below.

On 5 May, 1980, on three occasions, a radio-tagged yearling (40) flew towards three different females that were calling. He was displaced by four different territorial males in succession before encountering a banded, non-radio-tagged yearling male. Both approached and circled each other in threat posture for 20 s. Then the non-radio-tagged bird rushed at yearling 40 who flew and landed approximately 50 m away, where he was immediately displaced by another territorial male. These interactions took place over a 6 ha area during 1.8 h of observation. Yearling 40 was displaced by a territorial male on at least one other occasion (9 May) and was killed by a predator on 21 May. This type of behavior might explain this male's extremely large home range in comparison with other yearlings, and perhaps his subsequent death (see Jamieson 1982a). Furthermore, if the wide ranging movements of this bird prevented him from becoming familiar with an area and he was unable to develop site-dominance, that might explain his displacement by the other yearling.

Another interaction, on 15 May 1981, involved two radio-tagged yearlings whose home ranges were known. One (678) was away from his normal home range and was on an area where another (801) had frequently been found earlier in the season. Yearling 678 was feeding when 801 approached in a threat posture, pursued, and displaced him

from the area.

On 22 April, 1981, an incident was observed that involved fighting between two unbanded males. Although their ages could not be positively determined, these birds resembled yearlings because they appeared to be smaller and lighter in color than a banded adult male that flew into the area during the interaction, and they did not exhibit adult-like behaviors. Furthermore, no unbanded adults were seen or captured in this vicinity during the entire breeding period. Yearling 'A' approached 'B' from about 25 m. Both immediately paced in tight circles around each other in threat postures and gave threat calls (growls). Then, each faced the other, engaged in wing buffeting, and jumped at each other with their feet. This occurred four times until yearling B moved away, pursued by A. Then an adult male flew into the area and landed between the two yearlings. He rushed at B and both disappeared over a knoll with the adult in pursuit.

I observed 11 cases in which a yearling male interacted with a lone female. These were primarily initiated in one of two ways; males either walked or flew toward females that had been calling (N = 5), or they encountered them while moving about (N = 5); in the other case, a female flew into an area and a yearling flew to where she landed.

Upon approach, these yearlings assumed a full or partial display posture and exhibited "head bobbing" (Stirling and Bendell 1970) a few meters away from the female. They never dragged their wings or "whooted" (Stirling and Bendell 1970) as territorial males do during courtship. On three occasions, yearlings showed "displacement" behavior by suddenly moving away from the female and pecking at nearby bushes. Yearling males made no attempt to mount females and after 1-5 min of displaying, slowly returned to a neutral posture and began feeding. In cases where the responses of the females were monitored, they appeared disinterested and either remained still (N = 3) or fed (N = 4). In contrast to yearling males, adult males show a full range of courtship responses and frequently attempt to mount females, even relatively late in the breeding period when they are with broods. (F.C. Zwickel pers. comm.)

I observed five instances of yearling males interacting with both females and adult males. In these cases, yearlings flew from 40 to 100 m toward calling females that were on or near territories of adult males. They were immediately met by the resident males who courted the females only after they had chased the yearlings from the area.

Territorial and Singing Behavior of Yearling Males

Only one yearling showed what might be construed as territorial behavior during my study. This bird was "hooting", a territorial song (Stirling and Bendell 1970), during the day from 20–25 April in a 0.6 ha area. His home range was very small compared to other yearlings (Jamieson 1982a) but similar to that of territorial adult males (Lewis unpubl. MS He was not heard singing after 25 April but did interact and displace another yearling from this area on 15 May. After this date, his radio failed. The area was searched intensively with dogs for a two week period but he was not seen. He was located, however, by regular census crew on 20 May, 250 m from the center of his "territory". He was located two more times, later in the breeding season, 232 and 476 m from where he had localized in April. His home range during this period was similar to that of other yearlings. It appeared that he abandoned his territory sometime after 15 May.

Seven other instances of singing by yearling males, two by the same bird, were recorded. These occurred from 48 to 107 m from the nearest occupied territories. In two cases, which occurred during the day, singing was brief, but in others, hooting was soft and sporadic at first, then became louder and more continuous; these all occurred at dusk. Although only a few instances were noted, intermittent singing by yearling males may be more common than previously reported.

E. Discussion

Territoriality may be defined as the localization of a animal and exclusive use of that area (Pitelka 1959). In promiscuous species of grouse, territories allow males to attract, court, and mate with females without interference from other males (Bendell and Elliott 1967). Males that localize and perform behaviors related to territorial advertisement (for example, singing in Blue Grouse) are considered territorial.

In many species of grouse, however, first-year males do not occupy territories and, therefore, presumably do not breed (Wiley 1974). For example, in the sub-family Tetraoninae, yearling male Spruce Grouse (*Canachites canadensis franklinii*), Ruffed Grouse (*Bonasa umbellus*), and Blue Grouse usually do not exhibit territorial behavior (Herzog and Boag 1978; Gullion 1967; Bendell and Elliott 1967). In my study one of 24 yearling males appeared to be territorial, but for a very brief period only.

Yearlings have relatively large home ranges which may encompass several territories of adult males (Sopuck 1979; Jamieson 1982a). Also, first-year males rarely sing and are very secretive, associating with thickets during most of the day. Only at dusk do birds become more active in the open.

What factors are preventing yearlings from occupying territories and thus reducing their chances of breeding? Recrudescence of testes is delayed in comparison with adults, yet yearlings produce viable sperm (Hannon et al. 1979) and will occupy territories and sing if adults are removed (Bendell et al. 1972; Zwickel 1972, 1980). Testes of replacement yearlings are similar in size to those of non-territorial yearlings (Simard 1964; Zwickel 1980). Therefore, the usual absence of territorial behavior cannot easily be explained by gonadal immaturity.

The observation that yearling males do not breed, even though they can produce viable sperm, has been the focus of debate for many years (Verner 1964; Orians 1969; Selander 1972). Two major theories have been proposed to explain delayed breeding in yearling male grouse. In one, Wittenberger (1978) argues that breeding is delayed because first-year males cannot compete effectively for territories with older more experienced adults. Based on the "female choice" hypothesis (Orians 1969), Wittenberger contends that females should prefer to mate with territorial birds since they should have the highest genetic quality among competing males. My data confirm that adult males can

displace yearlings and prevent them from interacting with females that are on their territories. However, every year there are vacant territorial sites on the breeding range (Lewis and Zwickel 1981). In addition, some first-year males localize near these sites (Jamieson 1982a), but do not exhibit territorial behavior. Therefore, competition with adult males is not sufficient to explain why yearling males do not take territories on these unoccupied sites.

Another theory to explain why young males delay breeding is the "sexual bimaturism" hypothesis (Wiley 1974, 1981). Wiley argues that when the fitness of the male, but not the female, is increased by delayed reproduction, males may evolve deferred reproductive maturation and effort. Deferment of reproduction could be advantageous if early survival and later fecundity are increased. Wiley suggests that delayed maturation can increase subsequent fecundity if earlier reproduction entails diversion of resources that would be allocated for growth, as growth and size usually correlate with fecundity. Also, survival may increase if time and energy spent in reproductive activities, such as territorial maintenance and advertisement, can instead be devoted to feeding and hiding from predators.

Knowledge of time and activity budgets could indicate whether young, non-breeding males devote more time than adults to feeding, resting, and other activities contributing to individual maintenance. Yearling male Blue Grouse spend approximately one-third of their time feeding, and about three-quarters of their time sedentary, usually in or near vegetative cover during the day. They are active only for short periods at dawn and dusk, presumably when major potential predators such as diurnal raptors are inactive.

Although time and activity budgets for territorial males are not available, time spent feeding by adult and yearling males may not be critical since food does not appear to be limiting (Bendell and Elliott 1967). However, if territorial behavior increases conspicuousness and vulnerability to predators, as suggested by Wiley (1974), then territorial yearlings might have higher mortality rates then non-territorial, but localized yearlings. Lewis and Zwickel (unpubl. MS) found that non-territorial yearling male Blue Grouse suffer relatively low mortality and suggest that the advantage of their delaying breeding likely is related in part to low mortality and relatively long life expectancies. If mortality rates of territorial yearlings were higher, then why do yearlings take territories

if adult males are removed? Vacancies created by the removal of adults result in an unnatural situation in which the breeding rate of first-year males may increase enough to offset any increase in mortality. Therefore, it may be advantageous for yearlings to become territorial in a removal situation.

Wiley's (1981) second point is that social organization that provides the possibility of queuing for advantageous reproductive positions raises the possibility that deferment of reproductive activity results in increased fecundity at a later age. In other words, yearlings may not take territories in order to assess areas and perhaps associate with sites on prime habitat, thus increasing their chances of occupying one if it becomes available.

Lewis and Zwickel (1981) have suggested that territories of Blue Grouse may differ in quality as males on some sites had higher survival and better chances to breed than birds on other sites. They proposed that since males tend to use the same territory for life, it may be advantageous for a yearling to delay taking a territory until a high quality site is available. Some yearlings are found more frequently around certain territories than others, and they may be associating with high quality sites (Jamieson 1982a). Also, adults may not take a territory unless one of the sites with which they associated as a yearling becomes vacant.

Although birds may delay breeding as yearlings, intraspecific interactions, particularly those involving territorial males, may play an important role in the subsequent recruitment of these birds as adults into the breeding population. In spring, yearling male Spruce Grouse seem to be attracted to sites of advertising males (Nugent 1979). These birds made flights of unknown motivation onto territories and were immediately displaced by resident adult males. Nugent suggested that non-territorial birds may be locating preferred habitat in this manner, or may assess a resident for the potential of supplanting him from his territory. Similarly, some yearling male Blue Grouse may be initiating interactions with territorial males. Perhaps these birds are assessing territorial quality by testing the ability of the male to defend his site, if degree of aggressiveness is related to site quality.

If territorial sites do become vacant, then which non-territorial birds eventually settle there? To improve one's chances of obtaining a territory as a two-year old, it may

be advantageous for first-year males to exclude other yearlings from certain areas. In two encounters between yearlings that I observed, site-dominance may have had some effect on the outcome of the interaction; in another, overt fighting occurred. However, relatively few interactions among yearlings were seen as compared to those between yearlings and females or adult males.

Bendell and Elliott (1967) report that male Blue Grouse may threaten and fight when in contact, but that such behavior seems relatively rare on the breeding range. Singing and other auditory displays may separate territorial males. The secretive nature of yearling males may make detection by nearby birds difficult, so that few encounters within this age class occur. However, if an interaction between individuals does take place, it may serve to space those involved during the period of peak aggression. While yearlings were rarely seen together in early spring, they were found with other males on nine occasions late in the season, when aggression levels had declined (Jamieson 1982b). Six of the nine males were other yearlings, the rest were of unknown age. In contrast, first-year males interacted with females 16 times, and with territorial males 30 times early in the breeding season, but were only sighted near females four times late in the season. These changes in numbers of encounters with conspecifics could be due to temporal changes in relative densities of the different age and sex classes on the breeding range. However, most females and adult males remain on the study area until mid- to late August (F.C. Zwickel pers. comm.; Lewis unpubl. MS). Thus, in early spring, yearling males may be initiating interactions with females and territorial males, but may be avoiding birds of their own age and sex and of non-breeding status. This may explain why I saw very few interactions between yearling males.

Finally, even when an optimal life-history pattern involves a deferment of reproductive activities at early ages, an individual should never pass up opportunities to breed if risk and effort are low (Wiley 1981). Wittenberger (1978) notes that there is no evidence that yearling males who have access to receptive females defer breeding. Also, males that steal copulations on territories of other males have been observed in a number of species (Van Rhijn 1973; Le Boeuf 1974; Howard 1978).

In Blue Grouse, yearling males displayed to females that they encountered on or off territories of adult males, and therefore, risk and effort involved in this particular

behavior are assumed to be low. However, first-year males did not show the full range of courtship responses to females shown by adult males. Why they did not attempt to copulate, or why, in some cases, they quickly became disinterested in the female is unknown. In removal experiments, replacement yearlings sang, occupied territories, and presumably bred (Bendell et al. 1972; Zwickel 1972, 1980). However, no observational data were collected on their mating behavior and it is not known whether they showed the full range of courtship responses given by adults.

There may be three proximate factors affecting the mating behavior of yearlings: 1) they may not have developed or learned the full range of courtship behaviors (see Kruijt and Hogan 1967, p.234), 2) they are only motivated to elicit proper responses when females are in receptive postures, 3) acquisition of a territory is necessary before yearlings will show mating behavior similar to that of adults, or 4) a combination of 2 and 3. Until we determine under what conditions first-year males will attempt to breed, we can only speculate on why these birds usually defer reproduction in the wild.

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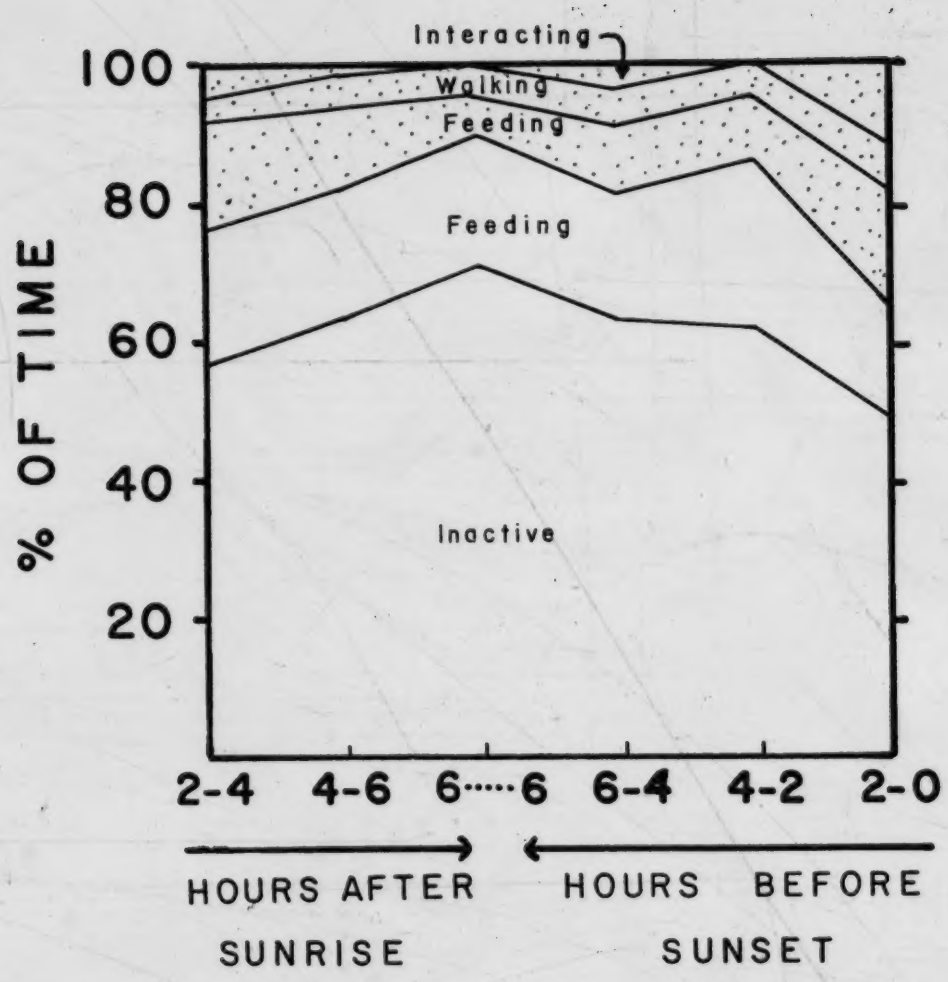

Figure 1. Percentage of time spent in various behavioral activities by yearling males. Stippling represents behaviors classified as moving; open represents those classified as stationary. Observations did not commence until two hours after sunrise.

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IV. CONCLUDING DISCUSSION

Many theories have been advanced to try to explain how numbers of animals in populations are regulated (see Krebs, 1978, for a general review). One of these, a behavioral hypothesis, suggests that mutual interactions involving spacing behavior among individuals produces changes in birth, death, and/or dispersal rates, and thereby prevents unlimited increase (Wynne-Edwards 1962). My studies were principally concerned with behavior that might be relevant to this hypothesis.

Early studies of Blue Grouse on Vancouver Island, particularly those involving experimental removal of breeding birds, indicated that behavioral interactions of territorial males in early spring may limit the number of yearling males that breed (Bendell et al. 1972; Zwickel 1972). My data confirm that adult males do displace yearlings that are on their territories and, therefore, it appears that first-year males are not able to compete effectively with older, more experienced males for breeding sites. However, the classical role that territoriality usually is said to play in the regulation process has recently been questioned, since vacant territorial sites always appear to be available on the breeding range (Lewis and Zwickel 1981). Results from more recent removal experiments indicate that males prefer certain territorial sites, presumably because of the potential for enhancing their survival and opportunities to breed (Lewis and Zwickel 1980). Lewis and Zwickel concluded that territorial quality may be the limiting factor in the regulation of numbers of adult male Blue Grouse and that yearling and some adult males may delay breeding until high quality sites are available.

Lewis and Zwickel (1981) argued that rather than select low quality sites, to which they may be committed for life, yearlings delay reproduction until they are adults, when chances of obtaining high quality sites are presumably increased. If site-specific experience as a non-territorial bird is important for successful territorial establishment, as suggested by some workers (Smith 1978; Yasukawa 1979), then yearlings that are surveying potential breeding sites should localize around high quality territories so that familiarity with these areas can be attained. One might predict from this that all birds should be associated with high quality sites as yearlings.

Unfortunately, on my study area I could not distinguish between high and low quality territories based on frequency of use, as Lewis and Zwickel (1981) had done.

However, while some yearlings were attracted to only a few particular territories of adult males, perhaps because these sites were of high quality, others localized near unoccupied sites that had been used as territories in the past. If these unoccupied sites are of low quality, then my results suggest that not all yearlings associate with high quality sites. Some may establish a territory on these unoccupied sites as two-year olds, irrespective of the availability of high quality territories in their second year. If all birds are not able to compete equally for high quality sites, then it may be advantageous for some to select low quality sites. Because of trade-offs in costs and benefits, perhaps yearlings associating with low quality sites have, on average, equal fitness to those associating with high quality sites. If so, then such a system might be maintained.

The above hypothesis assumes that those yearlings associating with high quality territories continue to do so as adults until one becomes available. This raises the question of why older males that fail to acquire high quality territories, would not settle on readily available low quality sites. Lewis and Zwickel (1981) suggest that since life expectancies decline with age, it may not be advantageous for older males to delay breeding, so some individuals who do not secure high quality sites then settle on those of lower quality and attempt to breed.

Adult males rarely changed territorial sites even when those of high quality were made available in removal experiments (Lewis and Zwickel 1980). Security may be enhanced by site familiarity, and territorial males may not move even though other areas are of higher quality. Similarly, yearlings that associate with certain territories may continue to do so until they can establish on a site that becomes vacated rather than risk going to an unfamiliar area. This may explain why 18 of 24 replacement males in the first year of a removal experiment were non-territorial adults and why 30% were over two years old (Lewis and Zwickel 1980).

Preliminary results in my study may also support the above arguments, as successful territorial establishment of birds associating with occupied sites appeared to depend on vacancies occurring within these territories. On the other hand, any yearling that localizes near an unoccupied site and that survives to the following spring should become territorial. This prediction may be verified after the fates of yearlings studied in 1981 are known.

It is important to note that the timing of recruitment of non-breeders may be season-specific. Therefore, any studies designed to examine this aspect of population regulation should be conducted at the appropriate times of the breeding season. My results on seasonal changes in spatial patterns and behavior indicate that the early breeding season, when aggression levels are highest, is most important in relation to subsequent recruitment of Blue Grouse. This may explain why the number of replacements to removal sites diminishes in late spring and early summer (Zwickel 1972, 1980; Lewis and Zwickel 1980). For other species, such as Red-winged Blackbirds, late breeding season may be critical for subsequent territorial establishment (Yasukawa 1979); variation among species may be related to differences in breeding biology.

Early in the breeding period, interactions involving yearlings and territorial males may play an important role in the eventual selection of a territorial site by a young adult. Some non-territorial birds may initiate interactions with adult males on their territories ; perhaps they are assessing territory quality by testing the ability of a male to defend his site. However, this still leaves the question of why yearlings that localize near unoccupied sites do not show territorial behavior, particularly if they are going to establish a territory there as a two-year old. Territorial advertisement and defence may increase conspicuousness and vulnerability to predators. If refraining from these behaviors as a yearling increases subsequent survival, then more secretive behavior may be selected for. Yearlings that do settle on unoccupied sites may actually show a gradient of behavior, ranging from very secretive to territorial. However, observations during my study and those of Bendell and Elliott (1967) indicate that those that do show territorial behavior as yearlings do so for only a brief period, perhaps during peak breeding only.

Finally, even though males may not occupy territories in their first year, these birds could potentially increase their fitness by attempting to copulate with females that they encounter. Even if females were not receptive towards yearlings, males could still gain valuable experience from such interactions. Yet, yearlings made no attempt to copulate and, after a brief period, appeared to become disinterested in the females. This is one aspect of the behavior of yearling males that remains puzzling.

In conclusion, while competition for territories in Blue Grouse appears to be a key factor in the regulatory process of breeding males, it alone does not explain why yearling

males do not breed. Results from removal experiments suggest that either territorial adults limit the number of yearlings that breed (Bendell et al. 1972; Zwickel 1972), or first-year males, in general, defer reproduction in order to increase their chances of obtaining a high quality territory as an adult (Lewis and Zwickel 1980, 1981). However, while yearlings that associate with high quality territories presumably do not occupy territorial sites for the latter reason, those that associate with low quality sites may delay breeding for other reasons such as increasing their chances of survival.

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